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Research Article

Climate-driven invasion risk and ecological niche overlap between non-native round goby and native European fishes

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Abstract

Biological invasions and climate change are two of the most prominent drivers of freshwater biodiversity loss. In this study, we assessed the climate-driven invasion risk and ecological niche overlap between the non-native round goby *Neogobius melanostomus* and several native European freshwater fishes (*Barbatula barbatula*, *Cottus gobio*, *Cottus perifretum*, *Cobitis taenia*, *Gobio gobio*, *Gymnocephalus cernua*, and *Perca fluviatilis*) to forecast shifts in their potential distributions using ecological niche modeling combined with future climate projections. Our models projected a substantial northward and westward expansion of *N. melanostomus* under future climate scenarios, with suitable habitats increasing especially under high-emission pathways. Native species also exhibited shifts in their distributions, often resulting in increased geographic overlap with *N. melanostomus*. Habitat overlap was most pronounced between *N. melanostomus* and *C. taenia*, with future projections identifying over 10% of the landscape as high-suitability. Overlap hotspots were concentrated in northern Europe, particularly along the coasts of the Netherlands, Germany and the UK, highlighting the potential for escalating biotic interactions such as competition, habitat displacement, and trophic disruption, particularly in vulnerable benthic communities. Alongside negative interactions, our results highlight potential climate refugia with limited projected overlap, pointing to priority areas for conservation. Our findings thus emphasize the urgent need for regionally targeted monitoring and conservation strategies that account for both climate-driven range dynamics and ecological interactions between invasive and native species. Integrating spatial forecasting with ecological risk assessment offers critical insights that can support efforts to mitigate the impacts of biological invasions in a warming world.

Key words: Biological invasions, climate change, ecological niche modelling, Europe, freshwater fish, invasive species, *Neogobius melanostomus*, niche overlap, species distribution

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Introduction

Biological invasions, i.e. the phenomenon describing the introduction, establishment, spread, causes, and consequences of human-mediated non-native species introductions outside their native range (Soto et al. 2024), present a considerable threat for nature and human well-being (Shackleton et al. 2019). This threat is exacerbated for freshwater ecosystems due to the close association with human activities (Dudgeon et al. 2006) as human settlements have historically been estab-

lished around freshwater, serving as critical sources of drinking water, food, energy, transportation, and recreation (Postel and Carpenter 1997). This long-standing reliance on freshwater systems has also increased the frequency and diversity of non-native species introductions, primarily via human-mediated pathways such as aquaculture, commercial shipping, recreational angling, the aquarium trade, and the construction of artificial canals connecting previously isolated catchments (Nunes et al. 2015; Bernery et al. 2024).

The visual inaccessibility of non-native species beneath the surface makes freshwater ecosystems also more susceptible to impacts of biological invasions occurring without being noticed (Reid et al. 2019). This includes, for instance, changes to trophic webs, habitat structure, community structure and ecosystem functioning (Ricciardi and MacIsaac 2011). The nature of freshwater ecosystems exacerbates these consequences as rivers form linear, dendritic networks that can facilitate the upstream and downstream dispersal of non-native species, thereby increasing the potential for successive establishments and thus, an expansion of the area affected by invasion impacts (Perrin et al. 2020). Moreover, lakes, ponds, and wetlands function as relatively isolated ecological islands, rendering them and their high degree of endemism susceptible to invasion impacts becoming irreversible (Havel et al. 2005; Leuven et al. 2009). Moreover, these insular bodies of water can paradoxically serve as stepping-stones for overland dispersal, especially when facilitated via flood events, canal systems, or deliberate releases (Ficetola et al. 2007; Keller et al. 2008), but also when the non-native invader is capable of overland movement (Rachalewski et al. 2013).

The round goby *Neogobius melanostomus*, native to the Black and Caspian Sea basins, is a non-native species known for its rapid spread across European and North American freshwater ecosystems (Kornis et al. 2012; Cerwenka et al. 2023). Following its rapid expansion, it has emerged as one of the most impactful non-native fish species in Europe, largely attributed to its high ecological plasticity and aggressive territorial behavior (Kornis et al. 2012; Cerwenka et al. 2023). In Europe, the round goby is invasive in major river systems such as the Danube, Rhine, and Elbe, as well as their tributaries, where its spread has been facilitated by canals and shipping routes linking previously isolated drainages (Cerwenka et al. 2023). Over the past two decades, its rapid range expansion has correlated with rising water temperatures, particularly within the Danube basin, where river regulation and other anthropogenic pressures have altered hydro-morphological and thermal regimes, reshaping fish communities (Harka and Bíró 2007; Bănăduc et al. 2020, 2023). The species' high phenotypic plasticity further enhances its capacity to exploit new habitats, driving both northward shifts and unpredictable westward colonization. Notably, round goby invasions can progress with exceptional speed, with populations becoming dominant in less than two years after introduction (Jůza et al. 2018). Numerous small-bodied benthic species native to Europe's freshwater ecosystems (such as *Barbatula barbatula* (Linnaeus, 1758), *Cottus gobio* Linnaeus, 1758, *Cobitis taenia* (Linnaeus, 1758), and *Gobio gobio* (Linnaeus, 1758)) occupy similar habitats and trophic niches as *N. melanostomus*, leading to significant ecological overlap (e.g., Piria et al. 2016; Janáč et al. 2018). Among the benthic species most threatened by the expansion of the round goby are bullheads (*Cottus gobio* and *C. perifretum* Freyhof, Kottelat & Nolte, 2005). Reports of their decline were published two decades ago (Jurajda et al. 2005) and have since been confirmed (e.g. van Kessel et al. 2016; Baer et al. 2017). In addition to the competitive advantage

of gobies over native bullheads, anthropogenic pressures such as increased siltation, channel modification, and water pollution also have adverse effects on these vulnerable populations (Knaepkens et al. 2002). Direct impact of round goby competitive superiority was observed in the Netherlands, where its rapid expansion led to severe decline in a *G. cernua* (Linnaeus, 1758) population (van Kessel et al. 2016). The presence of Ponto-Caspian gobies also affects *B. barbatula*, *C. taenia*, and *G. gobio*, and given that the round goby is the most expansive and efficient competitor among them, its impact on native species can be expected to be particularly strong (Grabowska et al. 2023). Invasive gobies have moreover been observed to monopolize shelter sites, preying on the eggs and juveniles of native fish, and altering benthic community structures through both direct interactions and broader ecosystem effects (Kornis et al. 2012; Grabowska et al. 2023). As climate change alters the environmental suitability of the European landscape, non-native species such as *N. melanostomus*, may expand their ranges into previously unsuitable regions (Harka and Bíró 2007; Kornis and Vander Zanden 2010; Błońska et al. 2024b).

The combination of *N. melanostomus*' wide distribution, rapid range expansion, and strong ecological impacts makes it a priority invader for assessing climate-driven invasion risks across Europe. However, while several studies have assessed the ecological impacts of *N. melanostomus*, few have integrated climate projections with spatial overlap analysis to evaluate risk to multiple native species at the continental scale (Reid and Ricciardi 2022; Le Hen et al. 2023), making modeling of potential shifts and quantifying overlap with native species crucial for anticipating future conflict zones and guiding conservation action (Emiroğlu et al. 2023). To this end, we use ecological niche modeling and future climate scenarios to assess the invasion risk posed by *N. melanostomus* to a suite of ecologically vulnerable native European fish species. Specifically, we (*i*) project range shifts under current and future climate conditions, (*ii*) quantify habitat overlap with native species across different climate scenarios, and (*iii*) discuss the ecological consequences and conservation implications of following interactions with native species in light of climate-driven invasion dynamics.

Methods

Data preparation

Species occurrence data

Among invasive Ponto-Caspian gobies, we focused on *Neogobius melanostomus* because it is the most widespread and ecologically impactful fish species in Europe, with stronger competitive dominance and broader distribution than other gobiids such as *Neogobius fluviatilis* or *Babka gymnotrachelus* (Cerwenka et al. 2023; Grabowska et al. 2023).

A set of native European fish species considered ecologically vulnerable to invasions by Ponto-Caspian gobies were identified based on the existing literature–including the review by Grabowska et al. (2023) as well as other relevant studies such as Jůza et al. (2018) and Błońska et al. (2025). This resulted in the inclusion of bullheads *Cottus gobio* and *Cottus perifretum*, stone loach *Barbatula barbatula*, gudgeon *Gobio gobio*, spined loach *Cobitis taenia*, ruffe *Gymnocephalus cernua*, and European perch *Perca fluviatilis* Linnaeus, 1758.

Species occurrence records for *N. melanostomus* and native fish species were retrieved from the "Global Biodiversity Information Facility" (GBIF; www.gbif.org). To ensure data quality, raw datasets underwent a multi-step cleaning process. Initial filtering using the CoordinateCleanerR package (Zizka et al. 2019) removed records with common spatial errors such as institutional coordinates (e.g. museums), zero coordinates, and capital city centroids. Additional manual cleaning eliminated records with missing coordinates, geographic outliers, and implausible locations (e.g. terrestrial points or duplicated records). To reduce spatial autocorrelation and sampling bias in species distribution models, spatial thinning was applied to each dataset using a rarefaction threshold of 5 km, implemented with thespThinR package (Aiello-Lammens et al. 2015).

Environmental data

Environmental predictors were obtained from the "WorldClim" 2.1 database (Fick and Hijmans 2017) at a spatial resolution of 2.5 arc-minutes (~5 km). This dataset included 19 bioclimatic variables and an elevation raster. Raster layers were cropped to the study area (longitude: -20° to 80°; latitude: 30° to 80°) and aligned to the elevation raster. Cells with missing values were removed to ensure consistency across layers.

Future climate data were sourced from Coupled Model Intercomparison Project Phase 6 (CMIP6) models for two time periods (2041–2060 and 2081–2100), considering two potential trajectories of shared socioeconomic pathways: SSP1-2.6 (low emissions) and SSP5-8.5 (high emissions) (Eyring et al. 2016). Then, five models were selected based on their performance in simulating hydrological and climatic variables relevant to freshwater ecosystems:

1. MPI-ESM1-2-HR: High spatial resolution; strong performance in modeling freshwater temperature and river dynamics (Gutjahr et al. 2019).
2. CNRM-CM6-1: Accurate in simulating precipitation variability and hydrological extremes (Voldoire et al. 2019).
3. IPSL-CM6A-LR: Reliable for simulating temperature and precipitation changes across Europe (Boucher et al. 2020).
4. HadGEM3-GC31-LL: High skill in modeling extreme climatic events and terrestrial hydrology (Williams et al. 2018).
5. EC-Earth3-Veg: Integrates vegetation, soil moisture, and hydrological processes (Döscher et al. 2022).

Variable Selection

A two-stage filtering process was used to reduce multicollinearity between environmental variables. First, buffer zones were created around each point to represent the environmental conditions around the species' geographical distribution points. Buffer zones were defined using the buffer function of theterra R package with a radius of 1 degree (~111 km) in WGS84 (EPSG:4326). This radius was chosen to characterize the large-scale environmental conditions of the species and to compensate for spatial uncertainties. Overlapping buffer zones were merged into a single geometric object. Climate and elevation raster data were then extracted from the merged buffer zone. Missing values (NA) were removed from the dataset, resulting in a clean data-

set for analysis. At the second stage, Pearson Correlation Analysis identified highly correlated pairs of variables ($|r| > 0.90$). For each correlated pair, the variable considered more ecologically relevant to freshwater fish distributions (e.g., temperature or precipitation variables over derived ratios) was retained, while the less interpretable variable was excluded (Dormann et al. 2013). Variance Inflation Factor (VIF) scores were calculated iteratively using the usdm package (Naimi et al. 2014) and variables with VIF > 10 were excluded. VIF measures the degree of multicollinearity among predictors, with higher values indicating redundancy; removing variables above the threshold reduces inflation of regression coefficients and improves model stability. This process resulted in an optimized set of three environmental variables for each native species distribution modeling, with the most influential predictors varying among species. It should be noted that TSS and ROC metrics were applied only for model performance evaluation and were not used during variable selection. Although species were parameterized with different subsets of variables, this does not bias interspecific comparisons because all models were calibrated under the same filtering framework and variable selection criteria, ensuring comparability in how climate constraints were represented. Temperature- and precipitation-related variables–such as BIO1, BIO3, BIO15, and elevation–weremost frequently selected (Table 1; Suppl. material 1: fig. S2a–h). Although the final set of predictors differed slightly among species, all were selected under the same filtering criteria, ensuring that the models remain directly comparable across species.

Species distribution modelling

Range shifts

Species distribution models (SDMs) were constructed using the BIOMOD2 R package (Thuiller et al. 2009; Thuiller 2023). This platform supports multiple modeling algorithms and ensemble forecasting. A total of 12 algorithms were used: Artificial Neural Networks (ANN; Haykin 1999); Classification Tree Analysis (CTA; Breiman et al. 1984); Flexible Discriminant Analysis (FDA; Hastie and Tibshirani 1996); Generalized Additive Models (GAM; Hastie and Tibshirani 1990); Generalized Boosted Models (GBM; Friedman 2001); Generalized Linear Models (GLM; McCullagh and Nelder 1989); Multivariate Adaptive Regression Splines (MARS; Friedman 1991); Maximum Entropy (MAXENT; Phillips et al. 2006); Maximum Entropy with R (MAXNET; Phillips and Dudík 2008); Random Forest (RF; Breiman 2001); Surface Range Envelope (SRE; Busby 1991); Extreme Gradient Boosting (XGBOOST; Chen and Guestrin 2016).

Table 1. Top three environmental variables contributing to each native fish species distribution models for each native fish species.

Species	Top Variable 1	Top Variable 2	Top Variable 3
Neogobius melanostomus	Elevation	BIO1 (Annual Mean Temperature)	BIO11 (Mean Temperature of Coldest Quarter)
Barbatula barbatula	BIO3 (Isothermality)	BIO15 (Precipitation Seasonality)	BIO18 (Precipitation of Warmest Quarter)
Cottus gobio	BIO15 (Precipitation Seasonality)	BIO7 (Temperature Annual Range)	BIO3 (Isothermality)
Cottus perifretum	BIO4 (Temperature Seasonality)	BIO15 (Precipitation Seasonality)	BIO1 (Annual Mean Temperature)
Cobitis taenia	BIO1 (Annual Mean Temperature)	BIO18 (Precipitation of Warmest Quarter)	Elevation
Gobio gobio	BIO1 (Annual Mean Temperature)	BIO15 (Precipitation Seasonality)	BIO3 (Isothermality)
Gymnocephalus cernua	BIO5 (Max Temperature of Warmest Month)	Elevation	BIO15 (Precipitation Seasonality)
Perca fluviatilis	BIO18 (Precipitation of Warmest Quarter)	BIO9 (Mean Temperature of Driest Quarter)	BIO15 (Precipitation Seasonality)

Model performance was evaluated using five-fold cross-validation. Predictive power was assessed using the True Skill Statistic (TSS) and the Area Under the Receiver Operating Characteristic Curve (ROC). Models with TSS and ROC values > 0.7 were retained for ensemble forecasting. Projections were made under current climate conditions and both future SSP scenarios. Raster processing and environmental data extraction were performed using the dismo R package (Hijmans et al. 2017). The ensemble approach enabled robust prediction of distributional shifts and identification of high-risk areas under climate change.

Habitat and niche overlap analysis

To assess potential interactions between *N. melanostomus* and native fish species, pixel-wise multiplication of habitat suitability raster was performed for all species pairs. The resulting overlap rasters were normalized to a 0–100 scale and classified into five categories: 0–20%, 20–40%, 40–60%, 60–80%, and 80–100%. For each overlap class, the proportion of pixels was calculated. These were visualized using histograms to represent current and future scenarios. This approach allowed identification of high-overlap zones, potential conflict areas, and anticipated shifts under projected climate change (e.g. Emiroğlu et al. 2023). All overlap analyses were calculated in R using the terraR package (Hijmans 2025).

Results

Current scenario

Under current climate conditions, model projections closely matched the known distribution of *Neogobius melanostomus*, with high suitability concentrated in the Ponto-Caspian region and major connected river basins across central Europe (Fig. 2). Native species also showed distributions largely consistent with their known ranges (Suppl. material 1: fig. S1). For some species, notably *Cottus gobio* and *Barbatula barbatula*, the models indicated relatively constrained suitable habitats under current conditions, suggesting narrower realized niches compared to more widespread species such as *Perca fluviatilis* or *Cobitis taenia*. These baseline distributions provide a reference for evaluating future shifts, as summarised in Suppl. material 2, which presents habitat stability, loss, and gain under SSP1-2.6 and SSP5-8.5 scenarios.

Range shifts

Ecological niche modeling predicted a noticeable northward shift in the potential distribution of *N. melanostomus* under both low (SSP1-2.6) and high (SSP5-8.5) emission scenarios. These shifts intensified in the late-century projections (2081–2100), especially under SSP5-8.5, indicating increasing climatic suitability across northern Europe (Fig. 1). Native species such as *C. taenia* and *P. fluviatilis* were also projected to expand their ranges westward or northward (Suppl. material 1: fig. S1). Notably, sympatric zones–where *N. melanostomus* overlapped with native species–became more pronounced in northern coastal regions, particularly the UK, the Netherlands, and northern Germany (Fig. 2).

Among the environmental predictors, isothermality (BIO3)–which reflects the ratio of diurnal to annual temperature variability–was one of the most influential

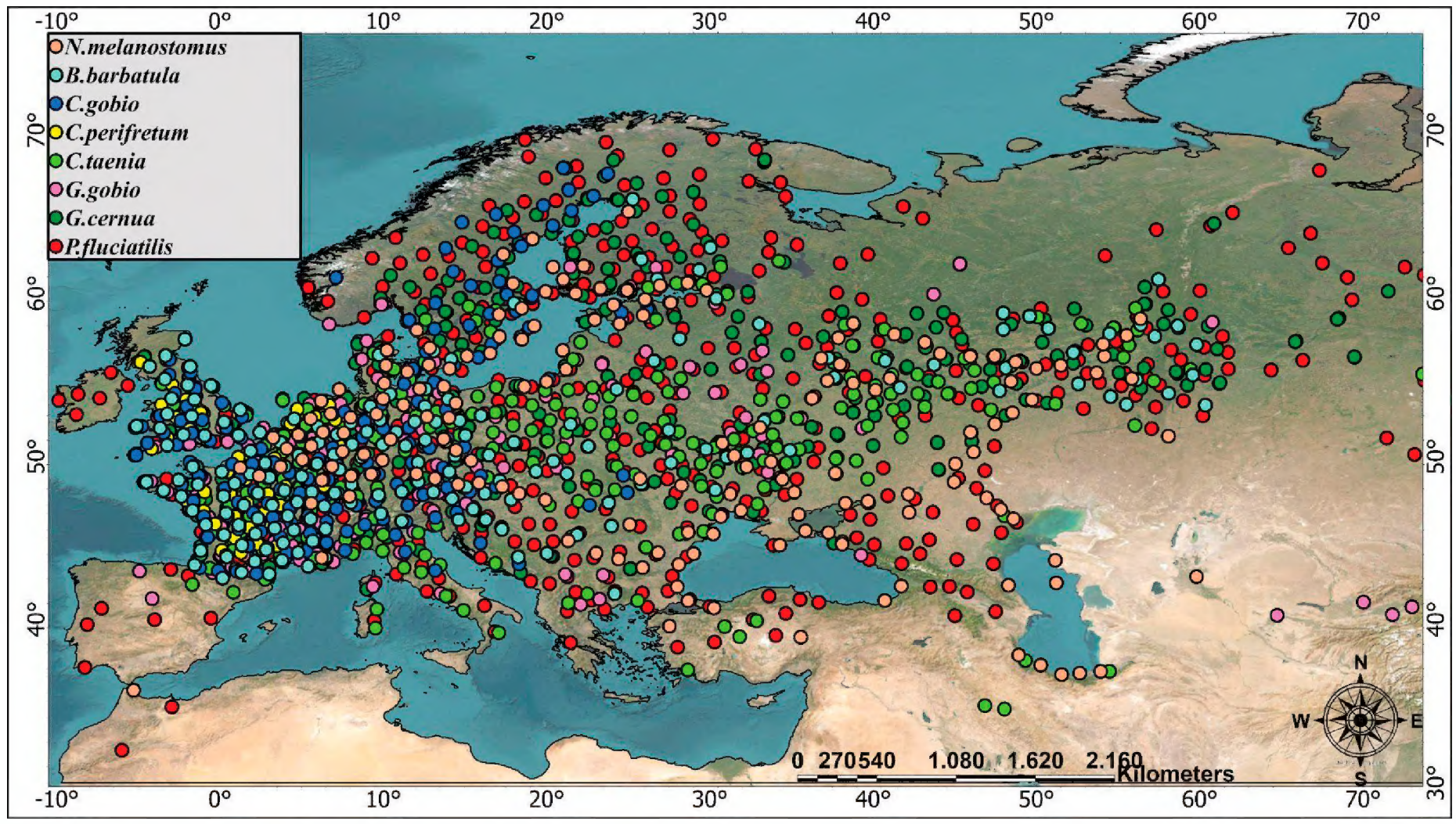

Figure 1. Distribution of *Neogobius melanostomus* and native species in the assessment area.

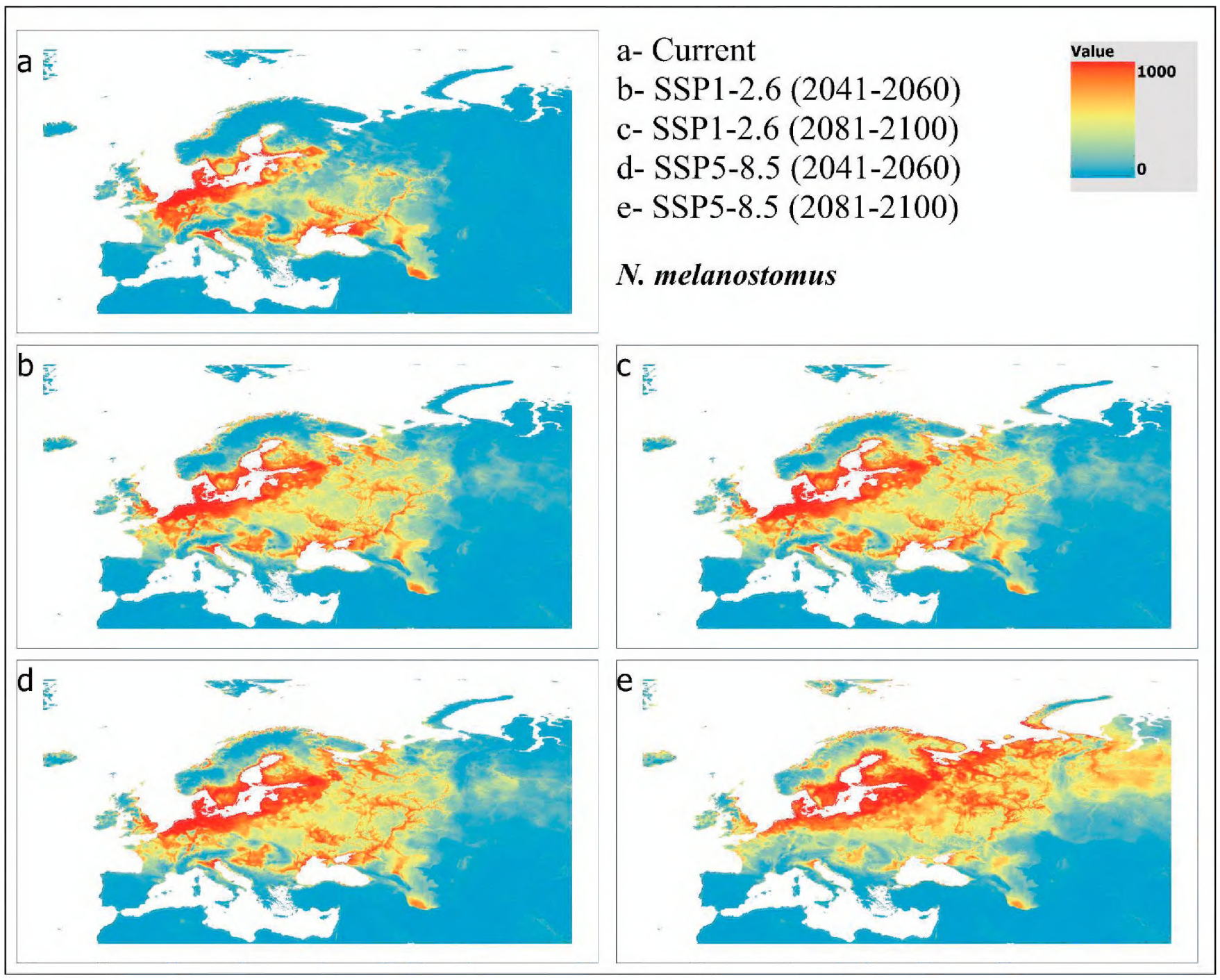

Figure 2. **a**. Present distribution of *Neogobius melanostomus* and predicted distributions under current conditions (SSP1-2.6) for **b.** 2041–2060 and **c.** 2081–2100, and future conditions (SSP5-8.5) for **d.** 2041–2060 and **e.** 2081–2100. Values are shown as a colour gradient, with blue (0) indicating minimum habitat suitability and red (1000) indicating maximum suitability.

variables shaping species distributions (Suppl. material 1: fig. S2a–h). It was particularly relevant for *N. melanostomus*, which favored areas with high isothermality, indicating a tolerance for environments with high daily thermal variability but relatively stable seasonal regimes (Suppl. material 1: fig. S2a). In contrast, several native species, including *B. barbatula*, *G. gobio*, *Gymnocephalus cernua*, and *P. fluviatilis*, were associated with low isothermality, indicating a preference for more thermally stable habitats (Suppl. material 1: fig. S2b–h). *Cobitis taenia* showed a broad tolerance, occurring across both high and low isothermality regions (Suppl. material 1: fig. S2e), while *Cottus perifretum* appeared largely insensitive to this variable (Suppl. material 1: fig. S2d). Elevation also played a significant role, generally exhibiting a negative relationship with habitat suitability across all species. This effect was strongest in *N. melanostomus*, which consistently avoided higher elevations, likely due to its adaptation to warmer, lowland environments (Suppl. material 1: fig. S2a). Other species showed similar, albeit less pronounced, patterns in response to elevation, reinforcing its broad importance in shaping freshwater fish distributions under current climate conditions.

With regard to future drivers, these patterns were largely consistent under future climate scenarios, with isothermality (BIO3) and elevation remaining the strongest predictors of habitat suitability for most species. However, for several natives such as *P. fluviatilis* and *G. cernua*, the relative importance of precipitation seasonality (BIO15) increased in future projections, suggesting that hydrological variability may play a greater role under warming conditions (Suppl. material 1: fig. S2).

These relationships were broadly consistent across current and future scenarios, with isothermality and temperature-related variables remaining the dominant predictors of habitat suitability under climate change. However, the relative influence of precipitation seasonality (BIO15) increased for several native species in future projections (Suppl. material 1: fig. S2), indicating that hydrological variability may become a stronger driver of distributional shifts under warming climates.

Niche overlap analysis

We first quantified current levels of spatial overlap between *N. melanostomus* and native fishes before comparing shifts under future climate scenarios. This approach allows us to distinguish increases in overlap caused by niche expansion of the invader, niche contraction of natives, or both. Under current climate conditions, the average spatial overlap between *Neogobius melanostomus* and native species was relatively low (<3%). The lowest overlap was observed with *Cottus perifretum* (0.6%), while the highest occurred with *Cobitis taenia* (4.7%) (Table 2, Fig. 3; Suppl. material 1: fig. S4). Under future climate scenarios–particularly SSP5-8.5 for 2081–2100–the average overlap increased modestly to around 5%. The highest projected overlap remained between *N. melanostomus* and *C. taenia* (7.9%), while *C. perifretum* continued to exhibit the lowest overlap, with over 96% of shared area falling into low suitability zones (0–20%) (Table 2; Fig. 4; Suppl. material 1: fig. S3). Under current climate conditions, overlap values were generally low (<3%), ranging from 0.6% for *C. perifretum* to 4.7% for *C. taenia* (Table 2; Fig. 3). By mid-century (2041–2060), overlap increased modestly under both scenarios. The strongest increases were projected under SSP5-8.5, with *C. taenia* and *P. fluviatilis* exceeding 5% overlap, while under SSP1-2.6, increases were more moderate and restricted mainly to *C. taenia* and *G. cernua* (Table 2; Fig. 4). By late century (2081–2100),

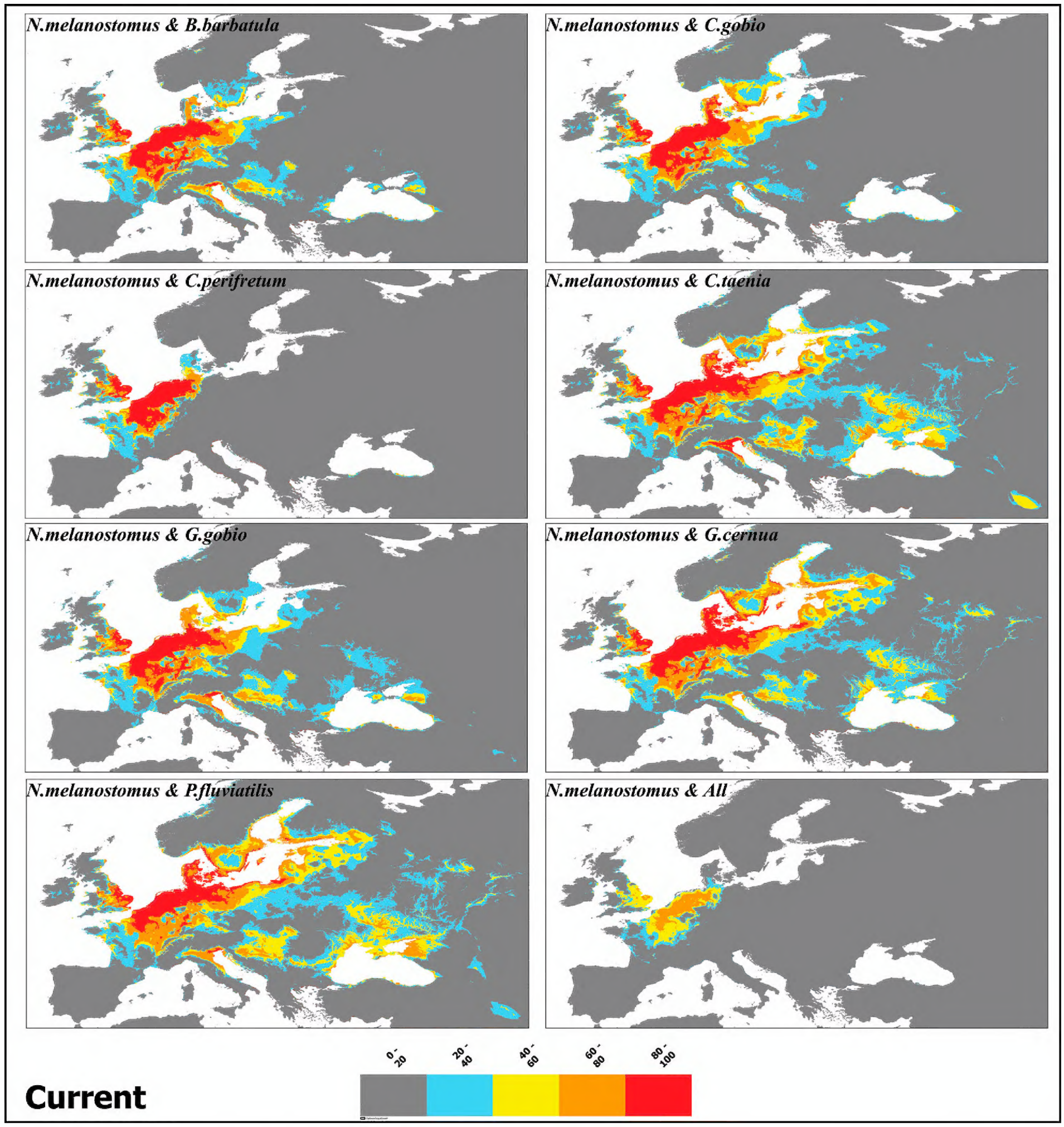

Figure 3. Prediction of overall niche overlap between *Neogobius melanostomus* and native species in the assessment area under current climate conditions.

overlaps became more pronounced, especially under SSP5-8.5, with *C. taenia* reaching nearly 8% and moderate increases observed for *G. cernua* and *P. fluviatilis*. In contrast, *B. barbatula*, *C. gobio*, and *G. gobio* consistently maintained minimal overlap with *N. melanostomus* across all scenarios (Table 2; Figs 3, 4).

Discussion

The range expansion of non-native fish species following ongoing human activity and climatic and environmental changes will present a major challenge for conservation efforts (Tickner et al. 2020). This is especially the case following the

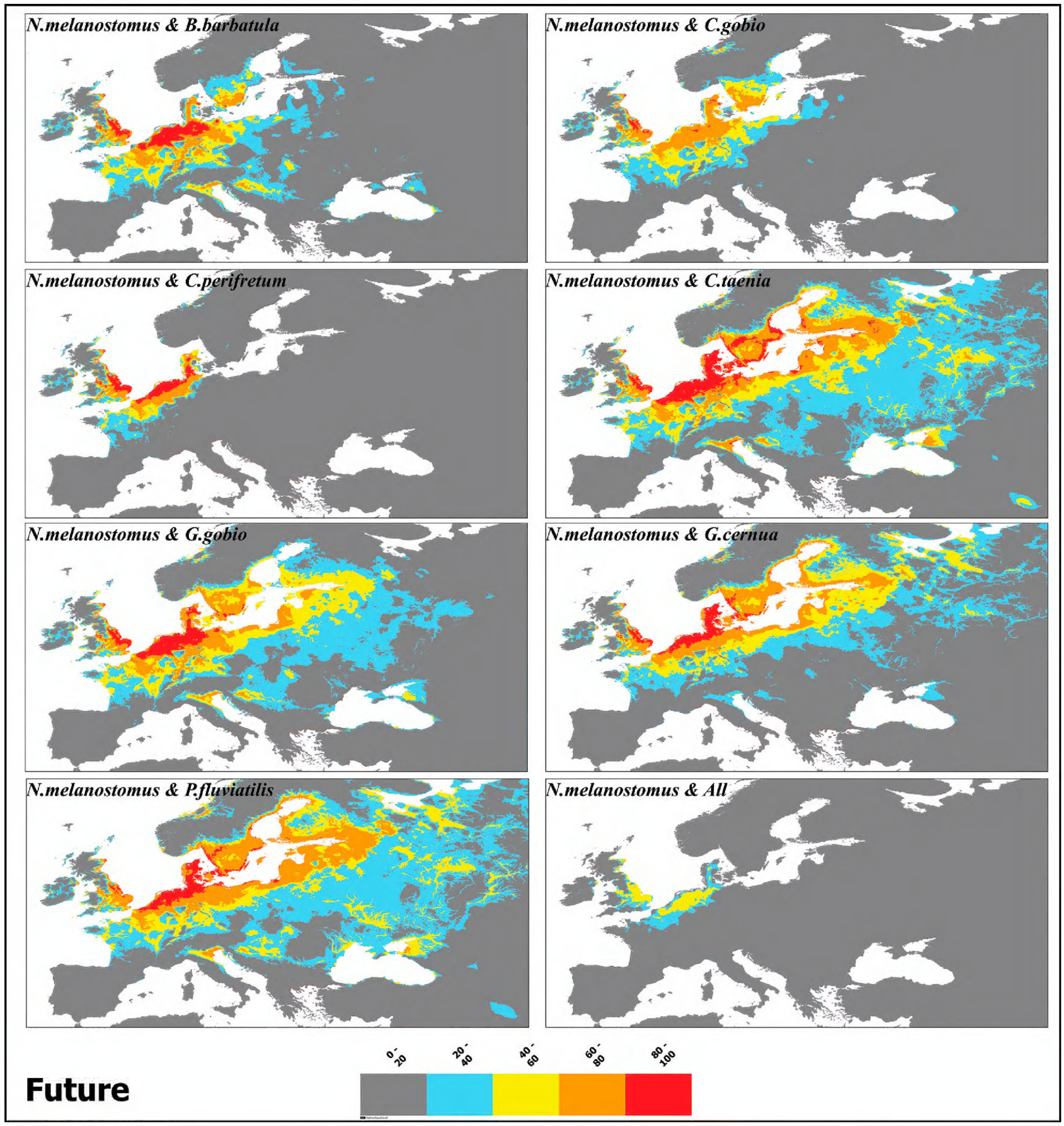

Figure 4. Prediction of overall niche overlap between *Neogobius melanostomus* and native species in the assessment area under future scenarios. Note that "future" refers to a combination of low- and high-emission scenarios (SSP1-2.6 and SSP5-8.5) for the periods 2041–2060 and 2081–2100, averaged across all future scenarios and timeframes.

spread of Ponto-Caspian species in Europe (Soto et al. 2023), having been linked to the decline of substantial freshwater biodiversity (Ricciardi and MacIsaac 2011). One of these detrimental Ponto-Caspian species is *Neogobius melanostomus*, which our results indicated will expand its range substantially into northern and western Europe, particularly under a pessimistic high-emission scenario (SSP5-8.5). Currently, *N. melanostomus* is already widespread across Europe, with self-sustaining populations in the Baltic Sea, Black Sea, Danube, Rhine, and Elbe basins, and has recently expanded into parts of the North Sea catchment (Kornis et al. 2012; Grabowska et al. 2023). Its present distribution overlaps with several native benthic

fishes, though current niche overlap values remain relatively low (<5%), providing a baseline for understanding future changes under climate change. The anticipated range shifts due to increasing climatic suitability further underlines that climate warming may act as a facilitator for this species' invasion, enhancing the likelihood of successful establishment of *N. melanostomus*, but also other thermophilic non-native species in temperate regions (Bellard et al. 2013; Capinha et al. 2015).

Range shifts

At present, *N. melanostomus* is already widespread across central and eastern Europe, with increasingly reported well-established populations elsewhere (Kornis et al. 2012; Cerwenka et al. 2023). Current overlap with native benthic fishes remains relatively low (<5%; see Table 2), indicating that although sympatry already occurs, the main component of invasion debt in this system relates to spread debt (Rouget et al. 2016)–the additional expansion of already established populations into climatically suitable but currently unoccupied habitats. Range shifts among freshwater fish, however, are emerging as a widespread response to climate warming, with both native and non-native species expanding their ranges poleward following shifts in thermal habitats and regimes (Chen et al. 2011; Rolls et al. 2017). In our projections, *N. melanostomus* and several native species exhibited clear northward expansions, though the extent and rate of these shifts varied. Such

Table 2. Percentage change in habitat overlaps between *Neogobius melanostomus* and selected native species under different climate scenarios. Overlap is reported by suitability classes, where 1 = 0–20% habitat suitability, 2 = 20–40%, 3 = 40–60%, 4 = 60–80%, and 5 = 80–100%. Positive values indicate increased overlap relative to current conditions, while negative values indicate reductions.

Native species	Climate scenario	Suitability class	Change in overlap (%)
Cobitis taenia	SSP5-8.5 (2081–2100)	4	117.3
Gobio gobio	SSP5-8.5 (2081–2100)	4	101.5
Perca fluviatilis	SSP5-8.5 (2081–2100)	4	98.8
Cobitis taenia	SSP1-2.6 (2081–2100)	4	55.9
Perca fluviatilis	SSP5-8.5 (2041–2060)	4	53.6
Cobitis taenia	SSP1-2.6 (2041–2060)	4	53.0
Gymnocephalus cernua	SSP1-2.6 (2081–2100)	4	51.5
Perca fluviatilis	SSP1-2.6 (2081–2100)	4	47.1
Gymnocephalus cernua	SSP1-2.6 (2041–2060)	4	47.0
Gymnocephalus cernua	SSP5-8.5 (2041–2060)	4	46.6
Cobitis taenia	SSP5-8.5 (2041–2060)	4	45.7
Perca fluviatilis	SSP1-2.6 (2041–2060)	4	45.0
Gobio gobio	SSP5-8.5 (2041–2060)	4	41.3
Gobio gobio	SSP1-2.6 (2081–2100)	4	37.2
Gobio gobio	SSP1-2.6 (2041–2060)	4	27.6
Cobitis taenia	SSP5-8.5 (2081–2100)	5	14.3
Barbatula barbatula	SSP1-2.6 (2081–2100)	4	11.8
Barbatula barbatula	SSP1-2.6 (2041–2060)	4	9.5
Barbatula barbatula	SSP5-8.5 (2041–2060)	4	6.3
Cottus gobio	SSP1-2.6 (2041–2060)	4	3.9
Cottus gobio	SSP1-2.6 (2081–2100)	4	3.5
Cottus perifretum	SSP1-2.6 (2081–2100)	4	2.3
Cobitis taenia	SSP1-2.6 (2041–2060)	5	0.6

movements may lead to novel community assemblages in northern ecosystems, potentially altering established food webs and competitive dynamics (Rolls et al. 2017). The expansion into previously uncolonized or isolated systems, including high-latitude lakes and headwater streams, raises concerns about ecological stability and resilience in these habitats (Ellender et al. 2015). Despite increasing climate suitability, southern range limits may remain relatively stable due to physiological constraints or lack of competitive advantage in warmer conditions (Comte and Olden 2017). However, our research on the physiological responses of *N. melanostomus* along a latitudinal gradient revealed the species' strong capacity for adaptation rather than a strict dependence on natural environmental gradients (Błońska et al. 2024b). Interestingly, temperature did not appear to be a key limiting factor–even for the southernmost population tested, which is likely exposed to frequent heatwaves and a high risk of heat stress (Błońska et al. 2024b).

Habitat and niche overlaps

Understanding the ecological consequences of biological invasions requires careful consideration of both projected niche overlap and the complex, context-dependent dynamics of species interactions because competitive impacts may not always be immediate or straightforward but may vary across spatial and temporal scales (Cerwenka et al. 2023). One of the most notable outcomes in this regard is that the potential niche overlap between *N. melanostomus* and native benthic fishes in future projections indicated an increase of >10% (in the case of *Cobitis taenia*). While this is indicative of elevated likelihood of direct competition for microhabitats and food resources (Uzunova and Dashinov 2022), it is crucial to consider recent findings that highlight context-dependent outcomes of non-native-native interactions. For example, Błońska et al. (2025) showed that non-native monkey goby *Neogobius fluviatilis* can coexist with native *C. taenia* without inducing significant displacement or competitive exclusion, possibly mitigated by habitat partitioning and behavioral flexibility. A similar situation has been observed for racer goby *Babka gymnotrachelus* and European bullhead *Cottus gobio* in the field (Kakareko et al. 2016) but not confirmed under experimental conditions (Kakareko et al. 2013; Grabowska et al. 2016). In the presence of the monkey goby, however, a relative decline in *G. gobio* was observed in the Sava River (Jakovlić et al. 2015), contrasting other studies conducted on the same river and at similar sampling (Piria et al. 2016). Aravind et al. (2022) demonstrated that the spread of invasive species tends to remain limited to areas that closely resemble their native environments, supporting the concept of niche conservatism–the tendency of species to persist within familiar ecological conditions.

This pattern indicates that invasion risks are highest in regions that are environmentally similar to a species' native range. These insights highlight the value of ecological niche models for predicting future invasions, even under climate change scenarios. To this end, our findings indicated that while *N. melanostomus* will expand northward, native species will also exhibit range shifts to higher latitudes. This parallel movement reflects niche conservatism in both invasive and native species, as each tends to track shifting climate envelopes rather than adapt to novel environmental conditions. As a result, future interactions are expected to intensify in regions where their ranges newly overlap–particularly in higher-latitude zones that maintain environmental characteristics similar to their historical

habitats. Finally, such increased overlap will also likely exacerbate competitive interactions for spawning sites, benthic shelters, and macro-invertebrate prey, where *N. melanostomus* has repeatedly demonstrated dominance over native taxa (Kakareko et al. 2013; van Kessel et al. 2016; Janáč et al. 2018; Jůza et al. 2018). This may lead to declines in reproductive success, reduced recruitment, and localized displacement of natives, particularly in fragmented or degraded habitats where escape options are limited.

Several native species, including *Cottus perifretum* and *Barbatula barbatula*, exhibited consistently low spatial overlap with *N. melanostomus*, even under high-emission scenarios. This suggests the existence of potential climate refugia, i.e. areas characterized by low suitability for *N. melanostomus* due to their thermal and elevational regimes, such as environments with stronger seasonal fluctuations or cooler highland habitats, thereby serving as critical strongholds for native species. Yet, their capacity to track suitable climates may be constrained by narrower thermal tolerances compared to non-native species, limited dispersal ability, and increasing habitat fragmentation in freshwater systems (Radtke and Bernaś 2025). This asymmetry in ecological plasticity could lead to competitive advantages for *N. melanostomus*, particularly in fragmented river systems and isolated basins where native species have less possibilities to avoid the invader (Dorenbosch et al. 2017). Such a disadvantage has been suggested in the case of the European bullhead, which is not only exposed to competition from Ponto-Caspian gobies but is also highly vulnerable to habitat modification and pollution (Błońska et al. 2016). Our results also highlight key environmental variables, especially temperature-related metrics and elevation indicative of potential vulnerability zones. For instance, species favouring environments with stronger seasonal thermal stability and lower daily variability (e.g. *B. barbatula*, *G. gobio*) may struggle under conditions of high diurnal fluctuations and shifting seasonal regimes, which in turn favour *N. melanostomus* and further intensify competitive imbalances, potentially including increased predation vulnerability due to loss of access to shelter (Błońska et al. 2017).

Management implications

Effective conservation of native fish communities in the face of climate change and goby invasions hinges on early detection, spatial prioritization, and adaptive habitat management (Błońska et al. 2024a). In particular, the importance of early warning systems and targeted monitoring (Reaser et al. 2020) in regions projected to experience high overlap, particularly coastal basins in the UK, the Netherlands, and northern Germany. Spatially explicit management, incorporating habitat conservation and restoration (e.g., connectivity enhancement), could help protect native species by buffering cascading impacts of both environmental and climate change as well as biological invasions (e.g. Dorenbosch et al. 2017), but may be limited/unfeasible due to their high costs (Stefanes et al. 2016) and often limited success (Sinclair et al. 2023). Importantly, while our study focuses on negative interactions, we also identified potential climate refugia–areas with minimal projected overlap–which could serve as critical conservation priorities. Supporting these zones through habitat protection and adaptive management strategies may represent one of the most viable approaches for maintaining native biodiversity under rapid environmental change. Ultimately, the combined pressures of climate change and biological invasions require a multidimensional, adaptive response. Tools like

the DOSI framework (Błońska et al. 2024a; Tarkan et al. 2024) that integrate dispersal dynamics, ecological impacts, and risk prioritization can be highly effective for proactive decision-making. Our study contributes to this growing body of predictive ecology, aiming to inform conservation planning before conflict between native and non-native species becomes irreversible.

Conclusion

Among the Ponto-Caspian gobies that are successfully expanding in Europe, *N. melanostomus* appears to be the most competitive–not only displacing native species but also outcompeting other non-native gobies (Grabowska et al. 2023). Our findings further demonstrate that climate change is likely to accelerate the range expansion of *N. melanostomus*, enabling it to spread into northern and western Europe, increasing its ecological overlap with several native benthic fish species. While some co-occurrence patterns may not immediately lead to displacement, as recent studies on *N. fluviatilis* suggest (Błońska et al. 2025), heightened competition for habitat and resources is probable, particularly for species with narrower thermal tolerances and limited dispersal capacity. By combining species distribution modeling, climate projections, and overlap analysis, we identify not only future conflict zones but also potential climate refugia. Recognising and supporting such refugia through habitat protection and adaptive management may be one of the most effective approaches to mitigate biodiversity loss under rapid environmental change. These results highlight the urgent need for spatially targeted management strategies that consider both invasion dynamics and climate-driven habitat changes. Overall, mitigating the dual threats of biological invasions and climate change will require integrated forecasting tools, proactive monitoring, and habitat-focused conservation planning–especially in vulnerable freshwater systems where opportunities for native species resilience are rapidly narrowing.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Use of AI

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Author contributions

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Data availability

All datasets used in this study are openly accessible and obtained from publicly available sources.

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Supplementary material 1

Supplementary figures and table

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Data type: pdf

Explanation note: **fig. S1.** Projected distribution of native species under current and future conditions for a) *Barbatula barbatula*; b) *Cottus gobio*; c) *Cottus perifretum*; d) *Cobitis taenia*; e) *Gobio gobio*; f) *Gymnocephalus cernua*; g) *Perca fluviatilis*. **fig. S2.** Response curves of environmental variables for a) *Neogobius melanostomus*; b) *Barbatula barbatula*; c) *Cottus gobio*; d) *Cottus perifretum*; e) *Cobitis taenia*; f) *Gobio gobio*; g) *Gymnocephalus cernua*; h) *Perca fluviatilis*. **fig. S3.** Contact zone probabilities of *Neogobius melamostomus* and other native species under current and future climate scenarios. **fig. S4.** Prediction of overall niche overlap between *Neogobius melanostomus* and native species (a: *Cobitis taenia*; b: *Barbatula barbatula*, c: *Cottus perifretum*, d: *Gobio gobio*, e: *Cottus gobio*, f: *Gymnocephalus cernua*, g: *Perca fluviatilis*) in different climate models. **table S1.** Habitat overlap rates (%) between *Neogobius melanostomus* and selected native species across different suitability classes under current and future climate scenarios.

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Supplementary material 2

Future SSP126 and SSP585 Climate Scenarios (2041–2060, 2081–2100): Habitat Status Categories (No Habitat, Stable, Gained, Lost).

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Data type: xlsx

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